Cormorants *Phalacrocorax carbo* breeding on the Norwegian islet of Måøya, part of the Sklinna archipelago, 5 May 2023. © *Svein-Hakon Lorentsen*

Timing of spring migration of Norwegian Cormorants *Phalacrocorax carbo*: long-term trends and effects of winter severity

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Abstract
Migratory birds are showing species-specific responses to climate change through changes in phenology, distribution and abundance. While many bird observatories collect standardised data on migratory passerines to provide invaluable information on changes in their abundances and migratory phenology, some bird observatories also undertake visual observations of passing migratory waterbirds and seabirds. In this study, we use two such long-term datasets of Cormorants *Phalacrocorax carbo* (hereafter 'Cormorant') compiled during their spring migration. We explore the extent to which winter severity has affected their migration phenology and whether there have been long-term trends in migration timing. Observations were conducted at Lista Bird Observatory in southwest Norway (1992–2020) and at Skagen in north Jutland, Denmark (1974–98). At Skagen, there were no detectable long-term trends in Cormorant migratory timing. However, the median date (marking the passage of 50% of birds) was significantly advanced following warm winters. Changes in the date of passage of the first 10% of birds was close to doing so as well, but the late phase (the passage of 90% of birds) showed no relation to temperature. At Lista, winter temperatures in the southern part of the wintering area had no significant effect on the overall timing of the spring passage, but the first 10% of the Cormorants migrated significantly earlier in years with mild late March temperatures at Lista. The early phase of passage at Lista showed a significant long-term trend towards an advancement of migration, leading to an extended migration period. The findings of this study indicate that the timing of Cormorant spring migration does in some cases respond to late winter temperatures or show long-term trends, but that the responses and trends differ between sites and between the beginning, middle and late phases of the migration, with the early and middle phases generally showing stronger responses and trends than the late phase.

Introduction
Due to anthropogenic climate change, global temperatures are rising at an accelerated rate, leading to milder winters and the earlier onset of spring (IPCC 2021). These changes have the potential to greatly affect bird populations via altered phenology, distributions and abundances (Møller *et al.* 2010; Knudsen *et al.* 2011; Lehikoinen *et al.* 2013; Stephens *et al.* 2016; Halupka *et al.* 2020). To obtain

a better understanding of how these changes are affecting bird populations, it is necessary to conduct long-term monitoring. A multitude of studies have attempted to investigate long-term trends in the arrival dates of birds and how they are affected by warming temperatures (e.g. Newson *et al.* 2016). A common theme in these studies is that phenological responses in migratory birds are often species-specific (e.g. Rubolini *et al.* 2007; Usui *et al.* 2017). The spring migration phenology of birds is well studied, and many species show long-term trends towards an advancement in arrival at breeding grounds, often correlated with higher spring or winter temperatures (Sparks 1999; Butler 2003; Cotton 2003; Rubolini *et al.* 2007; Usui *et al.* 2017).

Though bird migration is extensively studied, many studies focus on the date of the first arrival of one individual to their breeding grounds, thereby potentially being representative of a more extreme migratory period performed by an atypical individual. Trends in these dates may therefore not adequately represent changes in the migration phenology of the whole population (Miller-Rushing *et al.* 2008; Miles *et al.* 2017; Lehikoinen *et al.* 2019). First arrival dates have also been shown to be sensitive to changes in population size and observation effort (Sparks *et al.* 2001; Tryjanowski & Sparks 2001; Lindén 2011), meaning increasing population size might result in advanced first arrival dates even though the mean or median arrival dates remain unchanged. To obtain a better overall picture of changes in the migration phenology of a given population, long-term, systematic observations over the whole migration period and across multiple individuals are needed (Miles *et al.* 2017; Lehikoinen *et al.* 2019).

Although whole migration data series are relatively uncommon, systematic observations of migratory birds have been conducted over many years at some sites around the world, particularly in Europe and North America (e.g. Hüppop & Hüppop 2003; Marra *et al.* 2005; Miller-Rushing *et al.* 2008; Miles *et al.* 2017; Lehikoinen *et al.* 2019). These studies have illustrated that the early, middle and late phases of migration can have different, or even contrasting, long-term trends and differential responses to temperatures (Vähätalo *et al.* 2004; Miller-Rushing *et al.* 2008; Miles *et al.* 2017; Lehikoinen *et al.* 2019). For instance, when earlier phases of spring migration have advanced with time and show stronger responses to warm temperatures than later phases, birds will experience an extended migration period (Vähätalo *et al.* 2004; Miles *et al.* 2017; Lehikoinen *et al.* 2019).

For birds, the timing of migration and breeding can have profound fitness and reproductive consequences, with earlier arrival and breeding usually being associated with elevated reproductive success (Verhulst *et al.* 1995; Smith & Moore 2005; Sergio *et al.* 2007). One hypothesis for why early phases of spring migration often respond more strongly to warm temperatures than late phases, is that early-migrating individuals (most likely breeding adults in good condition) experience different selection pressures than late-migrating individuals (likely immature or other non-breeding individuals) (Vähätalo *et al.* 2004; Rainio *et al.* 2006; Lehikoinen *et al.* 2019).

Many studies using bird observatory migration data focus on passerines captured for ringing (e.g. Hüppop & Hüppop 2003; Marra *et al.* 2005; Miller-Rushing *et al.* 2008) but some are also based on visual observations of larger-bodied migratory species such as seabirds and waterbirds (e.g. Vähätalo *et al.* 2004). For example, Lista Bird Observatory, on the southwestern coast of Norway is a bird observatory that conducts long-term, systematic observations of migratory seabirds and waterbirds. Systematic observations of migrating and staging birds, as well as standardised trapping and ringing of passerines, have been conducted at Lista in both spring and autumn since 1990 (López *et al.* 2020). One of the species included in these observations is the Cormorant *Phalacrocorax carbo* (hereafter 'Cormorant'), a large migratory seabird and waterbird. Migration timing is important for Cormorants; their reproductive success decreases with later arrival at the breeding colony in spring, with strong selection for earlier arrival following warm winters and springs (Gienapp & Bregnballe 2012). Similarly, male Cormorants wintering closer to their breeding colonies have been found to arrive earlier and have higher lifetime reproductive success than males wintering further away (Bregnballe *et al.* 2006). By contrast, early arrival is likely less important for non-breeding immatures and first-year Cormorants, which tend to start their spring migration several weeks later than the adults (Bregnballe *et al.* 1997).

Although earlier arrival and shorter migration distances can lead to increased reproductive success in Cormorants, it can also have a cost. For example, Cormorants are vulnerable to low winter temperatures, and experience increased mortality during cold winters (Frederiksen & Bregnballe 2000; Herrmann *et al.* 2021), likely due to higher energetic requirements and the freezing of inland and coastal waters leading to reduced food accessibility (Herrmann *et al.* 2021). Due to their unique feather structure, Cormorants have a partly wettable plumage, which helps them in counteracting buoyancy when diving for fish, but which also substantially increases their energetic expenditure when diving in cold water (Grémillet & Wilson 1999; Grémillet *et al.* 2001; Grémillet *et al.* 2005).

We were interested to investigate a) whether large migratory seabirds like Cormorants, breeding along the Norwegian coast, showed a long-term trend towards earlier migration in spring, and b) to what extent preceding winter severity affected interannual variation in migratory timing. To do this, we used two long-term count datasets of spring migrating Cormorants: one from Lista Bird Observatory (during 1992–2020) and the other from Skagen, the northernmost tip of Denmark, (data from most years during 1974–98). We assume that the birds passing Skagen in spring will largely be the same individuals passing Lista in southwest Norway later the season.

We hypothesise that the timing of Cormorant spring migration will be affected by winter severity because high energetic expenditure during cold winters will constrain Cormorants from achieving sufficient body condition for migration and breeding, thus delaying their departure from winter quarters and spring staging sites. More specifically, we predict that early migrating Cormorants delay their

Plate 1. Adult and immature Cormorants *Phalacrocorax carbo* at Skagen, the northern tip of Jutland, May 2004. © *Knud Pedersen*

Plate 2. Juvenile, immature and adult Cormorants *Phalacrocorax carbo* at Skagen, October 2015. © *Knud Pedersen*

migration following cold winters, whereas Cormorants migrating later in spring will be less affected. Furthermore, because of increasingly milder winters and the earlier onset of spring, we hypothesise that the early migrating Cormorants will show a long-term trend towards an advanced spring migration, whereas Cormorants migrating later in spring will not.

Methods

Study species

The Cormorant is a large, colonial breeding, piscivorous waterbird (van Eerden *et al.* 2012). They have been recorded breeding in almost every country in Europe, with high densities around the Baltic Sea (Bregnballe *et al.* 2014). In winter, Cormorants disperse and are generally found at more southerly latitudes. Most individuals are migratory, but the distances travelled vary greatly between individuals (Bregnballe *et al.* 2006; van Eerden *et al.* 2012). There are two commonly acknowledged subspecies of Cormorant found in Europe, *P. c. carbo* and *P. c. sinensis* (Bregnballe *et al.* 2014). The *carbo* subspecies breeds in Norway, Iceland, northern Russia, Britain and Ireland, and France, and the total European breeding population is estimated to be around 42,500 pairs (Bregnballe *et al.* 2014). The *sinensis* subspecies has a much larger population size (well over 300,000 breeding pairs) and a wider breeding distribution, being found throughout most of continental Europe as well as in some parts of Britain and Ireland (Bregnballe *et al.* 2014). The *carbo* subspecies mainly breeds and winters along rocky and exposed marine coasts, but can also be found on inland waters, especially during winter (Mogstad & Røv 1997; van Eerden *et al.* 2012). The *sinensis* subspecies also uses coastal areas throughout the year but prefers more sheltered coasts and is found on inland waters to a much larger extent (van Eerden *et al.* 2012). The presence of a third subspecies has been suggested in Europe (Marion & Le Gentil 2006), but here we only distinguish between the two traditionally acknowledged subspecies.

Cormorants of both subspecies (*carbo* and *sinensis*) breed in Norway, but until 2015 their breeding distribution had not overlapped (Lorentsen 2014a; Lorentsen *et al.* 2021). *P. c. carbo* breeds on islets along the Norwegian coast, from the Russian border in the north to Hordaland in western Norway in the south, with the majority breeding in central and northern Norway (Lorentsen 2014a; Lorentsen *et al.* 2021). *P. c. sinensis* has a much more recent history in Norway, having first bred in the country in 1996 (Lorentsen *et al.* 2021). Since then, the breeding population of *sinensis* has grown steadily to around 2,500 pairs in 2012, with a breeding distribution confined to the southern and southwestern coast of Norway (Lorentsen 2014b; Lorentsen *et al.* 2021). For comparison, the breeding population of *carbo* was estimated at 19,000 pairs in 2012–14 (Lorentsen 2014a; Lorentsen *et al.* 2021). In autumn, *P. c. carbo* start moving south towards their wintering areas, which mainly includes the coasts of central and western Norway as well as the Skagerrak and Kattegat (Mogstad & Røv 1997). In contrast, *P. c. sinensis* breeding in Denmark and Norway overwinter largely in western and central Europe, both inland and along the coast, and may also be found in Denmark, along the western coast of Sweden, and along the southern and southwestern coast of Norway (Bregnballe *et al.* 2021).

Counts of migrating Cormorants

The data used in this study come from observations of migrating Cormorants that were conducted at Lista Bird Observatory (58°11'N 6°56'E) in Norway and Skagen (57°72'N 10°58'E) in Denmark during the spring (Figure 1). Lista Bird Observatory is situated on the southwestern coast of Norway and systematic observations of migrating and staging birds have been carried out there between 15 March and 10 June every spring since 1990. The counts are conducted from the shore every morning after sunrise and continue until migration activity ceases. Counts and heading directions of all migrating bird species are recorded. The counting method follows a systematic routine, but the effort and number of observation hours can vary slightly between days, depending on the number of personnel and the amount of migration activity; we predict that this will have minimal impact on the results of this study. For further information on the methods used see Wold *et al.* (2012) and Ranke *et al.* (2022). Due either to a lack of staff or lack of focus on seabird counting during the first two years of observation (1990–91) the observations from these years were less systematic than in the following years and were therefore excluded from the analyses of this study (Figure A1, see online Supplementary Materials). Furthermore, to include only Cormorants moving in a direction relevant for spring migration, analyses were limited to birds seen migrating towards the northwest (i.e. along the coast towards breeding colonies further north; hereafter referred to as 'northward migration').

Observations conducted at Skagen, the northernmost tip of the Jutland peninsula in Denmark, were somewhat less systematic than those from Lista, as counts were not necessarily conducted every day during the spring migration period (particularly during early spring). Observations of migrating Cormorants at Skagen were recorded during continuous observations of all migratory waterbird species. The observations started at sunrise and typically continued for most of the day, or for at least 4–5 hours. The number of hours with continuous observation therefore varied from day to day, but we have not been able to correct for this variation because the information on the exact timing of the start and end of the recording of migration does not exist for all days. However, most Cormorants passed by during the early morning and so we believe that on days when counts were conducted, most Cormorants would still have been recorded. At Skagen, the observations cover the years 1972–98, with the exception of 1992. Information on the exact number of observation days each year is lacking,

Figure 1. The two sites from which the observations of migrating Cormorants *Phalacrocorax carbo* used in this study were conducted: Lista Bird Observatory in Norway and Skagen Bird Observatory in Denmark.

but the number of days when at least one Cormorant was observed was recorded (Table A1; Figure A2, see online Supplementary Materials). Counts were conducted from various sites along the coast of Skagen, particularly Grenen, Skagen Nordstrand and Skagen Harbour. The heading of Cormorants observed migrating past Skagen was recorded and analyses were limited to those migrating in a northerly direction.

Since the Norwegian *carbo* population was larger than the *sinensis* population (of which comparatively few birds breed north of Lista) during the study period (Lorentsen 2014b; Lorentsen *et al.* 2021), most Cormorants observed migrating past Lista towards the northwest in spring likely belong to the *carbo* subspecies. Furthermore, since the *sinensis* subspecies first bred in Norway in 1996 (Lorentsen 2014b; Lorentsen *et al.* 2021), the Cormorants seen migrating past Skagen and towards the north in spring in the years covered by this study (1972–98) should mainly be of the *carbo* subspecies.

Temperature data
To analyse the effects of winter severity on the timing of Cormorant spring migration, mean air temperature data in January–March each year (1972–2020) from Skagen Lighthouse were investigated. This was considered a representative weather station to encompass the winter distribution of Cormorants migrating past Skagen and Lista in spring, most of which likely winter in Skagerrak or Kattegat (Mogstad & Røv 1997). We chose the January–March period as a compromise between capturing the full cumulative effects of the whole winter and focusing on conditions closer to the migration itself, arguing that a warm late winter period could potentially 'mask' the effects of a cold early winter period on the birds' body condition (and vice versa). Furthermore, the mean temperature in January–March was highly correlated with the mean in February–March (Pearson's r = 0.94, P < 0.001, N = 49) and with the mean in December–March (Pearson's r = 0.96, P < 0.001, N = 49), indicating that the exact definition of the winter period would not alter the results.

Data analyses
For all analyses and both locations (Lista and Skagen) the data were confined to observations of migrating Cormorants made between 15 March and 31 May each year. Because of variation in coverage and observation effort between years, only years that had a minimum of 20 days between 15 March and 31 May where at least one northward migrating Cormorant was observed, were included from Skagen. This criterion led to the exclusion of the years 1972–73, 1976–80, 1992 and 1996 at Skagen (Figure A2, see online Supplementary Materials). For both Lista and Skagen, we determined the date of passage of the first 10%, 50% and 90% of all the migrating Cormorants observed each year, representing the early, middle and late phases of the spring migration, respectively (as in Jonzen *et al.* 2006). The 10th and 90th percentiles were chosen rather than 5th and 95th percentiles (Vähätalo *et al.* 2004; Lehikoinen *et al.* 2019) as they were more robust in years when the sample size was modest and less likely to be affected by the considerable

stochasticity in the number of Cormorants passing each day. Similarly, the duration of the migration period was measured as the number of days between the passage of the first 10% and the first 90% each year (Miles *et al.* 2017).

Linear regression was used to investigate the possible effects of winter severity on the timing and duration of Cormorant spring migration at each location. The dates of the early, middle and late passage phases and the duration of the migration period were response variables, and the mean January–March temperature was an explanatory variable. Similarly, linear regression with year as an explanatory variable was used to investigate possible long-term trends in both the dates of passage and the duration of the migration period at each location. Visual inspection of residual plots was used to checked for homoscedasticity and the normality of residuals for all models. All statistical analyses were performed in R Version 4.1.3 (R Core Team 2022).

Results

The spring passage of Cormorants was concentrated over a shorter period at Skagen in Denmark (mean duration = 32.1 days ± 10.7 SD, N = 18) than at Lista Bird Observatory in Norway (mean duration = 50.7 days ± 6.4 SD, N = 29). At Skagen, minimal northward migration was observed until late March and thereafter migration intensity increased progressively until it peaked in mid April (Figure A3, see online Supplementary Materials). Migration activity at Skagen dropped rapidly after mid April and then decreased more slowly from late April until the end of May. At Lista, northward migrating Cormorants were recorded from around the middle of March and the intensity of migration steadily increased until it peaked around 10 April (Figure A4, see online Supplementary Materials). After a short and sudden decrease at Lista during mid April, migration activity then remained relatively stable until end of May. This difference between the two sites is also evident when comparing the dates of passage of the first 10%, 50% and 90% of all the migrating Cormorants (Figure A5, see online Supplementary Materials). The two sites follow a somewhat similar pattern between years, but the late phase always passed Skagen 2–3 weeks earlier than at Lista, with the reverse being true for the early phase in some years when early migrating Cormorants passing Skagen a few days later than at Lista. Often ten or fewer individuals were seen at both Lista and Skagen (Figure A6; Figure A7, see online Supplementary Materials), however, the proportion of days when more than 100 Cormorants were observed migrating, was much higher at Skagen (11.3%) than at Lista (1.8%). The maximum number of migrating Cormorants observed in a single day was 665 at Skagen and 423 at Lista (Table A1, see online Supplementary Materials).

At Skagen, a considerable proportion (18% and 34%, respectively) of year-to-year variation in the timing of passage of the early (first 10% of Cormorants) and middle (50% of Cormorants) phases of the spring migration could be explained by winter temperature in the area (Figure 2a). Date of passage of the first 50% of Cormorants at Skagen showed a significant, negative, linear relationship with the mean air temperature of January–March (slope = -1.11, R^2 = 0.34, t = -2.89, P =

0.011, N = 18), with birds tending to pass earlier following warm winters. Date of passage of the first 10% of Cormorants showed a similar relationship with the mean air temperature of January–March, although this was not significant (slope = -1.15, R² = 0.18, t = -1.86, P = 0.082, N = 18). In comparison, the date of passage of 90% of Cormorants and the duration of the migration period seemed unaffected by winter temperature (P = 0.556 and P = 0.599, respectively, and N = 18 for both). At Skagen, none of the dates of passage nor the duration of the migration period, showed significant long-term trends (P > 0.05 and N = 18 for all; Figure 3a).
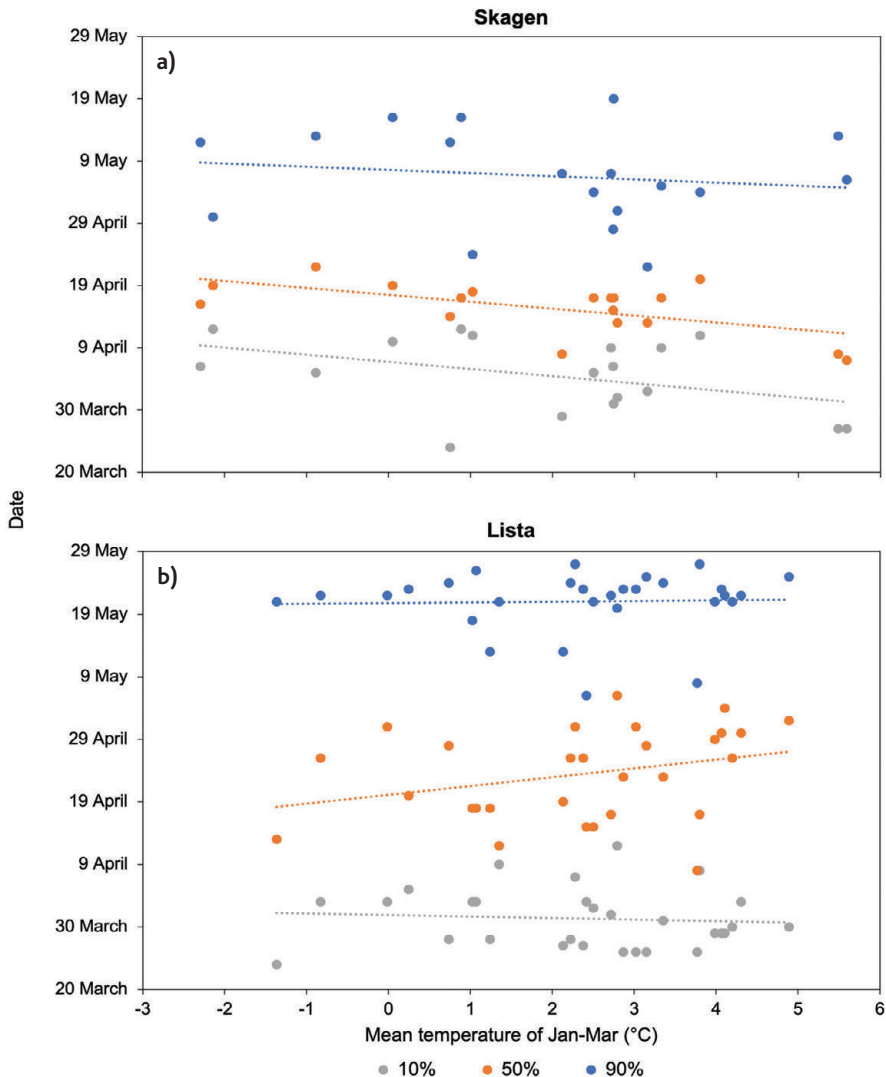

Figure 2. The relationship between the date of passage of the first 10%, 50% and 90% (representing the early, middle and late phases of the spring migration, respectively) of all the northward migrating Cormorants *Phalacrocorax carbo* observed at a) Skagen (Denmark) and b) Lista (Norway) during the period 15 March to 31 May each year, and the mean air temperature at Skagen in January to March each year.
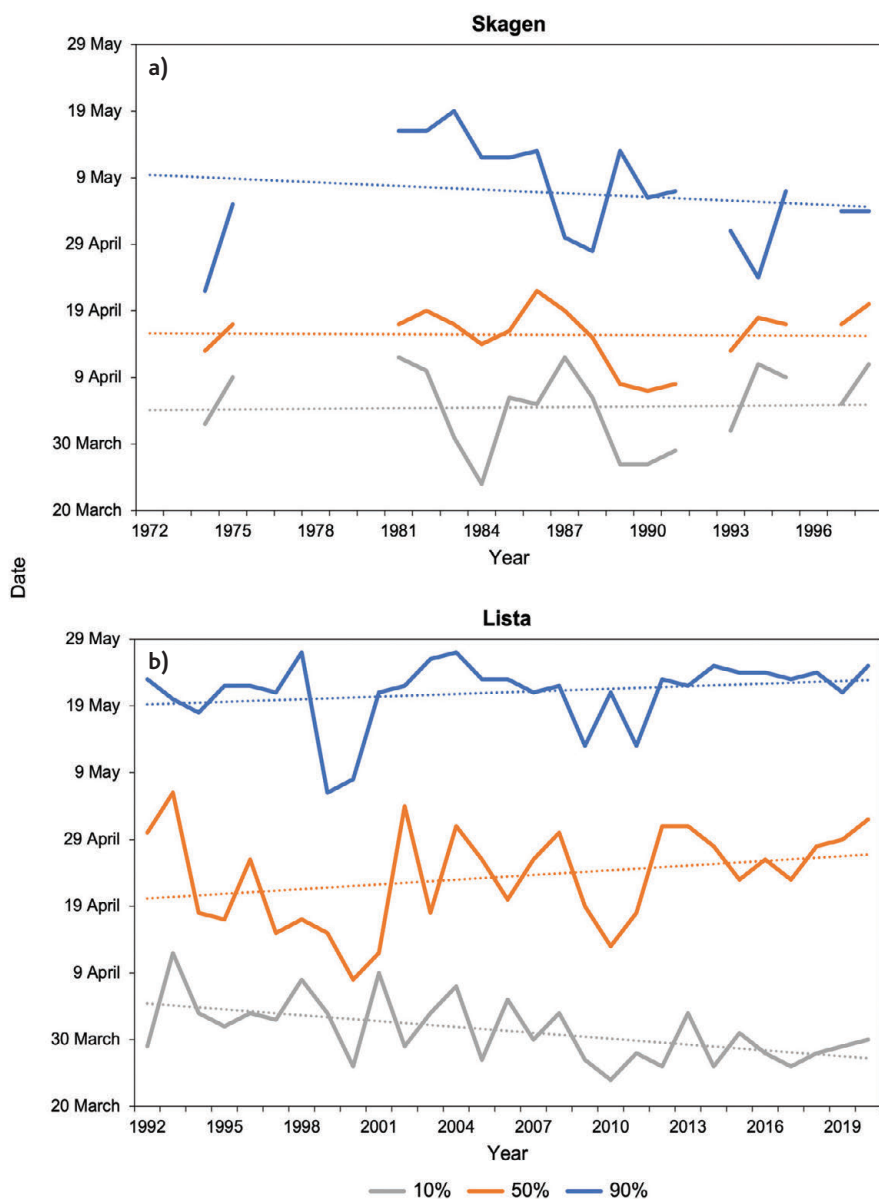
Figure 3. The date of passage of the first 10%, 50% and 90% (representing the early, middle and late phases of the spring migration, respectively) of all the northward migrating Cormorants *Phalacrocorax carbo* observed at a) Skagen (Denmark) and b) Lista (Norway) between 15 March and 31 May each year.

The relationship between the severity of winter and the timing of passage at Lista was unclear (Figure 2b), as neither the dates of passage nor the duration of the migration period showed a significant relationship with the mean air temperature in January–March ($P > 0.05$, $N = 29$). In order to explore whether the timing of passage at Lista was more related to the immediate and local temperatures than

with the average winter temperature in the wintering area in Kattegat, we also looked at the timing of passage at Lista in relation to the mean air temperature at Lista during the second half of March (16–31 March), i.e. around the time when early birds tend to pass Lista. The timing of passage of the first 10% of Cormorants at Lista was significantly earlier in years with mild temperatures in the second half of March (slope = -1.16, R^2 = 0.22, t = -2.75, P = 0.011, N = 29; Figure 4), although no relationship was found for the middle and late migration phases (P > 0.05, N = 29 for both).

The trend observed among early migrating birds at Lista deviated from those of the later migrating individuals (Figure 3b). The passage of the first 10% of Cormorants showed a significant trend towards being earlier (slope = -0.29, R^2 = 0.27, t = -3.17, P = 0.004, N = 29), passing Lista on average 2.9 days earlier each decade. The timing of passage of both the first 50% and 90% of Cormorants was not significant (slope = 0.24, R^2 = 0.07, t = 1.47, P = 0.152, N = 29 and slope = 0.13, R^2 = 0.05, t = 1.16, P = 0.256, N = 29 respectively). Combined, this led to a significant increase in the duration of the migration period (slope = 0.42, R^2 = 0.31, t = 3.52, P = 0.002, N = 29) which expanded, on average, by 4.2 days per decade. A marginal positive trend in the mean air temperature in January–March at Skagen was detected over the study period, 1972–2020 (slope = 0.036, R^2 = 0.07, t = 1.90, P = 0.064, N = 49). The lack of significance in this relationship was driven by three consecutive warm winters during the very first years of the study period (Figure A8, see online Supplementary Materials).
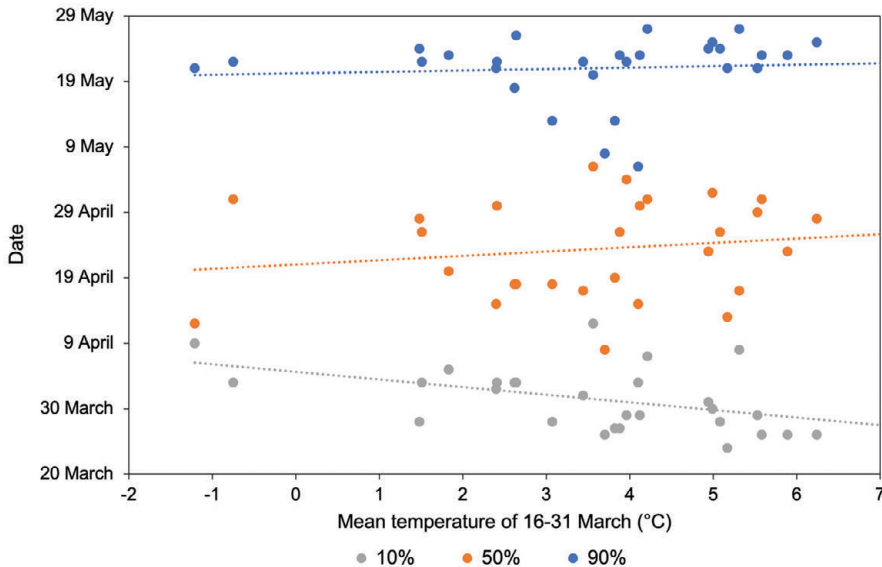

Figure 4. The relationship between the date of passage of the first 10%, 50% and 90% (representing the early, middle and late phases of the spring migration, respectively) of all the northward migrating Cormorants *Phalacrocorax carbo* observed at Lista (Norway) during the period 15 March to 31 May each year, and the mean air temperature in 16–31 March at Lista.

Discussion

Here we demonstrate that the migration of Cormorants can, at least in some cases, be affected by winter temperatures. For example, the passage of the first 50% of migratory Cormorants to pass Skagen (Denmark) was earlier after milder winters. Whilst the passage of the first 10% of Cormorants seemed to follow a similar relationship, this was less clear due to high inter-annual variation and lower observation effort in early spring. On average, Cormorants were seen 1.1 days earlier for every degree increase in winter temperature (January–March), a stronger relationship than that observed in a longer-term, multi-species study that reported increases of 0.7 and 0.5 days for every degree increase in spring temperature (Lehikoinen *et al.* 2019). The date when 90% of the Cormorants had passed Skagen was unaffected by winter temperatures. This lack of response to temperature amongst late-migrating Cormorants was unsurprising and likely due to them being immature birds (Bregnballe *et al.* 1997) that would therefore not suffer the negative consequences of late arrival to breeding grounds that breeding adults would (Gienapp & Bregnballe 2012). Similar patterns have previously been described across multiple species across Europe and Canada; in response to warmer spring or winter temperatures earlier phases of migration generally advance more than later phases (Vähätalo *et al.* 2004; Lehikoinen *et al.* 2019).

The Cormorants observed in this study were mainly Norwegian *carbo*, which overwinter along Norway, Denmark, and the western coast of Sweden (Mogstad & Røv 1997). During severe winters, this subspecies is less likely to be influenced by frozen inland waters and reduced food accessibility but will instead likely experience heightened thermoregulatory costs when diving in cold waters, due to their partially wettable plumage (Grémillet & Wilson 1999; Grémillet *et al.* 2001; Grémillet *et al.* 2005). This being said, by increasing their foraging efficiency and minimising the time spent in the water, Cormorants are still capable of balancing their energetic budgets, even in Arctic conditions (Grémillet *et al.* 2001). However, difficulties in locating high prey density areas can make it harder for Cormorants to balance their energy requirements during particularly cold winters (Grémillet & Wilson 1999; Grémillet *et al.* 2001), especially when competition is high (Herrmann *et al.* 2021).

In contrast to that at Skagen, the timing of the Cormorant spring migration at Lista was not related to the mean temperatures experienced at the wintering area of Kattegat (here represented by the January–March temperatures in Skagen). However, the timing of the passage of the earliest migrating birds at Lista (the first 10%) was instead related to the temperatures recorded at Lista around the time when the early birds would usually pass there. It is possible that some of the Cormorants migrated towards the breeding areas in several steps, adjusting the timing of their final migratory steps with the climatic conditions experienced at the stopover sites, rather than those further south where they spent the winter. Another possibility is that the weather station at Skagen poorly reflected the conditions that were experienced in winter by the majority of the birds that were passing Lista very early in spring, i.e. a proportion of the birds passing Lista probably

spent the winter along the Norwegian coast of Skagerrak rather than further south in Kattegat (Mogstad & Røv 1997). Birds wintering closer to their breeding areas could be expected to respond faster to mild weather in the northern areas than those wintering further south (Bregnballe *et al*. 2006).

Despite the effect of winter temperatures on Cormorant spring migration phenology at Skagen, we did not detect significant long-term trends in the overall timing of their migration during 1974–98. Although not statistically significant, the temperature parameter used in this study showed a positive trend over the whole study period (1972–2020), a trend similar to that observed at other North European locations in early spring (Lehikoinen *et al*. 2019). Contrastingly, the first 10% of Cormorants passing Lista showed an advancement in the timing of their migratory passage during the 1992–2020 period which led to a significant increase in the duration of the entire spring migration period. Similar patterns have also been described for other species, with early phases of migration generally showing long-term advancing trends while later phases show weaker and, in some cases, opposite trends, thereby increasing the length of the migration period (Miles *et al*. 2017; Lehikoinen *et al*. 2019).

Long-term, standardised ringing schemes and the systematic counting of migrating birds across the whole migration period, are methods considered to provide reliable data for studying bird migration phenology (Dunn 2016; Miles *et al*. 2017; Lehikoinen *et al*. 2019). Despite this, standardised programmes can have practical limitations (Knudsen *et al*. 2007). We acknowledge the limitations of the lack of standardisation in the data collection in this study, as well as the challenges in comparing data from two different locations, with differing levels of observer effort, during different time periods. Despite taking place for a varying number of hours each day, the counts of Cormorants used in this study were conducted in the morning, coinciding with the peak in Cormorant migration activity (Flore & Hüppop 1997; Hüppop *et al*. 2010). We therefore believe that any variation in observation effort between days is likely to have had minimal influence on our results. This being said, inferences regarding the phenology of migration can be influenced by single days with abnormally high observations of Cormorants and are likely due to a combination of both variable observation effort as well as the true nature of Cormorant migration. For example, Cormorants tend to migrate in flocks (Flore & Hüppop 1997; Hüppop *et al*. 2010) and their numbers can vary greatly with wind direction (Krüger & Garthe 2002). We therefore encourage caution when interpreting migratory phenology data gathered in this way.

In conclusion, systematic observations of migratory birds from bird observatories provide valuable data for studying the migratory phenology of species not otherwise included within passerine trapping and ringing schemes. Long-term, systematic observations like these are particularly timely for aiding our understanding of how bird populations are responding to a rapidly changing climate. Cormorants can be easily observed and counted during their spring migrations and this study demonstrates that, despite their large body size, they can

be affected by winter severity. At Skagen in Denmark, the middle phase of Cormorant migration significantly advanced following warm winters (January–March), and at Lista in Norway, the early phase of passage advanced during years of high local temperatures in late March. Furthermore, early-migrating Cormorants showed a long-term trend towards earlier passage at Lista, thereby increasing the duration of the population's migration period.

Acknowledgments

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Supplementary Materials

The Supplementary Materials for this article are available online at: www.seabirdgroup.org.uk/journals/seabird-35/seabird-35-e-appendices.pdf